

Evaluating the Efficiency of a One-Square-Meter Quadrat Sampler for Riffle-Dwelling Fish

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Abstract.—We evaluated the efficacy of a 1-m² quadrat sampler for collecting riffle-dwelling fishes in an Ozark stream. We used a dual-gear approach to evaluate sampler efficiency in relation to species, fish size, and habitat variables. Quasi-likelihood regression showed sampling efficiency to differ significantly ($P < 0.001$) among species of four common fish families (Cyprinidae, Ictaluridae, Cottidae, and Percidae) but not among species within each family ($P > 0.05$). Sampling efficiency was significantly influenced by physical habitat characteristics. Mean current velocity negatively influenced sampling efficiencies for Cyprinidae ($P = 0.009$), Cottidae ($P = 0.006$), and Percidae ($P < 0.001$), and the amount of cobble substrate negatively influenced sampling efficiencies for Cyprinidae ($P = 0.025$), Ictaluridae ($P < 0.001$), and Percidae ($P < 0.001$). Water temperature negatively influenced sampling efficiency for Cyprinidae ($P = 0.009$) and Ictaluridae ($P = 0.006$). Species-richness efficiency was positively influenced ($P = 0.002$) by percentage of riffle sampled. Under average habitat conditions encountered in stream riffles, the 1-m² quadrat sampler was most efficient at estimating the densities of Cyprinidae (84%) and Cottidae (80%) and least efficient for Percidae (57%) and Ictaluridae (31%).

Riffle habitats generally possess high, species-rich densities of benthic fishes in warmwater streams (Coon 1987; Kessler et al. 1995), yet they are challenging habitats to sample effectively. High current velocities make seines difficult to handle, and when electrofishing, wash stunned fish out of the electrical field before they can be captured (Bayley and Dowling 1990). The riffle habitat's large substrate sizes (e.g., boulders and cobble) also decrease one's ability to capture fishes by providing refuge from electrofishing and seining (Lyons 1986).

Regardless of habitat, the efficiency of sampling gear is also influenced by the size and species of fish (Bagenal 1979; Reynolds 1996). In general, larger fish tend to be more vulnerable to capture with electrical gear, whereas smaller fish are more difficult to capture, possibly because of the hy-

pothesized lower voltage differential that runs across them (Buttiker 1992). Smaller fish are, however, more vulnerable to collection with a seine, apparently because larger fish are more successful at avoiding capture (Bayley and Dowling 1990). Species-specific behaviors, such as vertical position in the water column, can also affect the vulnerability of a fish to capture. Failure to account for differences in sampling efficiency introduces a systematic error or bias into the data that can significantly affect fish-density and richness estimates and the interpretation of fish-distribution and habitat-use patterns (Bayley and Dowling 1993).

Previous investigations of riffle-dwelling fishes have attempted to reduce the influence of sampling bias by using a variety of maximum-effort methods, such as multiple-removal (i.e., depletion) sampling (Schlosser 1981; Bart 1989) or mark and recapture. Maximum-effort techniques require several sampling runs (i.e., passes) and can be expensive and time consuming. However, spatial and temporal variations among fish samples are often very high and require collection of large numbers of samples to obtain reliable density estimates (Pe-

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terson and Rabeni 1995). Thus, maximum-effort methods, coupled with high sampling frequencies, may be cost prohibitive. In addition, recent investigations suggest that density estimates derived from these techniques may also be biased (Buttiker 1992; Rodgers et al. 1992; Riley et al. 1993; Anderson 1995).

Some investigators have used or evaluated prepositioned area electrofishers (Bain and Finn 1991; Weddle and Kessler 1993; Bowen and Freeman 1998), hand seines (Lotrich 1975), or direct observation (Greenberg 1991) to study benthic fishes; however, none of them took into account the efficiency of the gear or the influence of physical habitat characteristics. For instance, Weddle and Kessler (1993) compared the efficiency of their gear relative to kick-seining but did not examine the influence of physical habitat characteristics on sampling efficiency. Similarly, Ensign et al. (1995) compared abundance estimates of three benthic species from distance sampling, line transect, and electrofishing in a quadrat and found them to be correlated. However, they did not examine the influences of physical habitat or species on sampling efficiency. Fisher (1987) evaluated the relative effectiveness of a benthic fish sampler in riffles of three Kentucky streams and found significant differences among seasons. Our study builds on Fisher's (1987) effort by examining the influence of physical habitat on efficiency as well as the effects of fish size and species.

To obtain reliable species-richness or density estimates for riffle-dwelling fishes, we believe the best sampling strategy includes collecting a large number of samples with the most cost-effective methods for which sampling biases are known. Unbiased estimates of fish density can then be obtained by adjusting raw catch data with estimates from sampling-efficiency models (Buttiker 1992; Bayley and Dowling 1993; Anderson 1995). Thus, we evaluated the 1-m² quadrat sampler (Rabeni 1985) as a riffle-dwelling, fish sampling gear with the following objectives: (1) to determine ease at which samples can be collected, (2) to investigate the differences among species and the effects of physical habitat characteristics on quadrat sampling efficiency, and (3) to synthesize sampling-efficiency models.

Methods

Study areas.—We evaluated the sampler on 25 riffles along two different-sized reaches of the Jacks Fork River located in Texas and Shannon counties, Missouri. The Jacks Fork is a typical

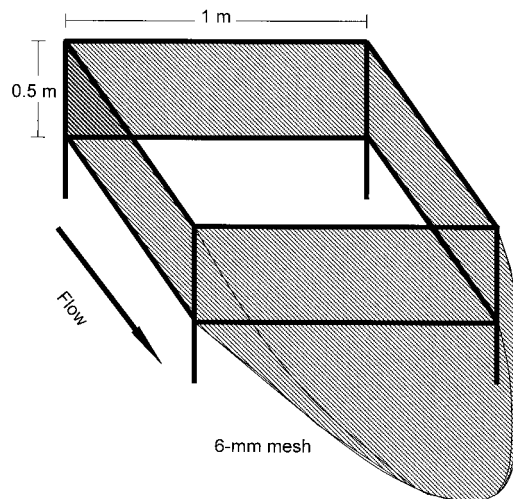


FIGURE 1.—The 1-m² quadrat sampler used to sample riffle-dwelling fishes.

Ozark Plateau stream with broad, rolling uplands incised by deep river valleys. The streambed is composed primarily of chert gravel and coarse sand as well as some boulders and cobble in areas adjacent to limestone bluffs or in high-gradient sections. The upstream site was a third-order reach on the North Prong of the Jacks Fork River and the downstream site was a fifth-order reach in the Ozark National Scenic Riverways. Discharges during the study averaged 1.02 m³/s at the upstream site and 6.73 m³/s at the downstream site.

Design and operation.—The 1-m² quadrat sampler consisted of two 1-m² frames attached 0.5 m apart to 0.75-m-long pipes, which resulted in 0.25-m-long legs at the bottom (Rabeni 1985). The front and sides of the sampler were covered with 6-mm-mesh netting, and a 0.75-m-deep collection bag was attached to the back of the sampler (Figure 1). We experimented with several designs and found samplers made with 2.54-cm² pipe to be the most rugged.

Fish were collected with the quadrat sampler by trapping them within the sampler and driving them into the collection bag. The standardized procedure involved collection of individual quadrat subsamples by placing the sampler in a riffle, securing it to the streambed, and disturbing the substrate within the sampler by kicking. This dislodged fish and moved them into the collection bag. Starting at the downstream end of a riffle, individual quadrat subsamples were collected at uniform intervals longitudinally and laterally to ensure good cov-

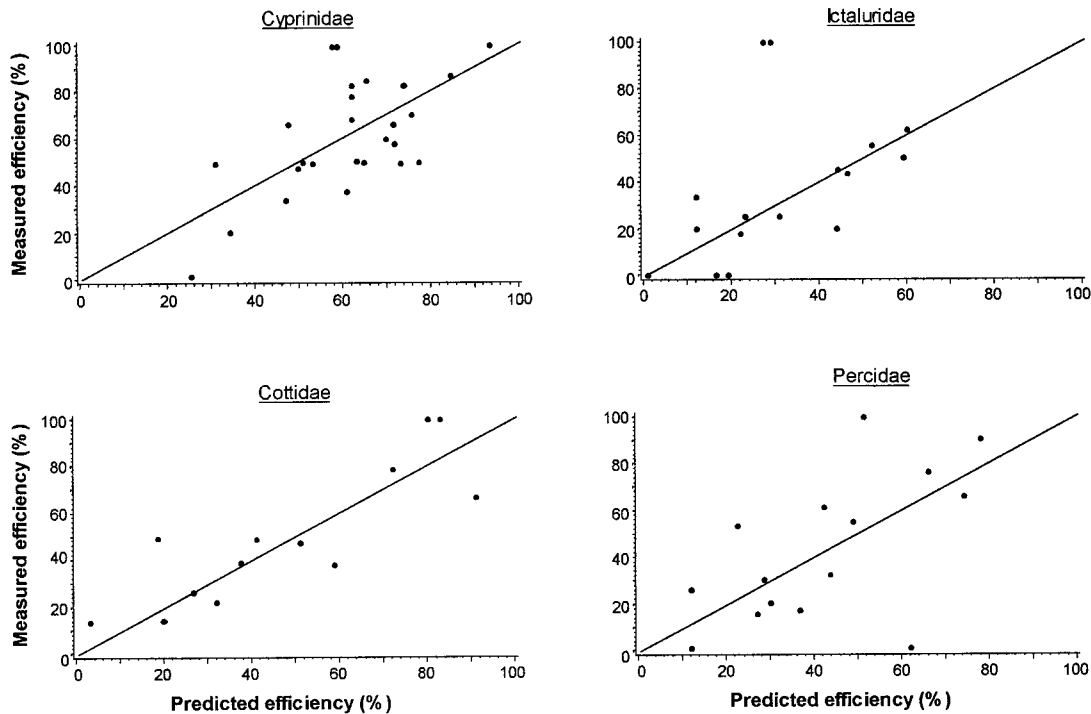


FIGURE 2.—Predicted and measured sampling efficiencies of the electric seine by family group in riffle and race habitats in the Jacks Fork River, Missouri; data are from Peterson (1996). Diagonal lines represent perfect model fit. All measurements were made in blocked-off sections of streams. Predicted sampling efficiency is based on sampling-efficiency models, and measured sampling efficiency is based on the capture of known numbers of individuals in the blocked-off areas. Note that more than 90% of observations for all family groups were within the 95% confidence limits of the sampling-efficiency predictions.

erage of the entire riffle (Peterson and Rabeni 1995).

Calibration procedure.—Sampling efficiency is the percentage of fish or species in a given area that are captured during sampling. Consequently, our efficiency calibrations required a reliable estimate of the actual fish abundance (or number of species) in a given riffle. Repeated sampling methods (e.g., removal, multiple mark-recapture) could not provide reliable estimates because these estimates are influenced by such factors as fish species and size (Buttiker 1992; Anderson 1995) and the physical characteristics of the area sampled (Rodgers et al. 1992). Therefore, we used a dual-gear calibration procedure (detailed below) in which a closed population was sampled with a primary gear (quadrat sampler) followed by a secondary gear (electric seine) that has a known ability to estimate the true population. Efficiency of the primary gear was then estimated by using secondary-gear catch data, adjusted for sampling efficiency, as the baseline. The success of this approach de-

pends upon the accuracy of estimates from the secondary gear.

The efficiency of the electric seine was thoroughly evaluated in Illinois streams by Bayley and Dowling (1990), and their resulting gear-efficiency models were verified and adjusted for Ozark species by Peterson (1996); both are presented for each of the four family groups in Figure 2. Thus, the electric-seine catch data, adjusted for differences in efficiency (see below), provided reliable estimates of actual fish abundance in the blocked-off riffles and were used as the standard to which we compared the quadrat sampler. It should be noted that this baseline is based on an estimate of the actual number of fish in the blocked-off area; hence, there is a variability to the data that may not be explainable by the covariates. This procedure was used successfully to evaluate various fish collection methods (Bayley et al. 1989; Bayley and Austen 1990; Bayley and Dowling 1990) and has been shown to provide reliable abundance estimates (Peterson 1996).

We conducted all calibrations during daylight hours on randomly selected dates between March 1992 and late October 1994. The calibration procedure consisted of blocking off entire riffles with 6-mm-opening mesh nets that were secured to the streambed. The dimensions of the blocked-off area were such that they simulated a nonblocked-off habitat (i.e., the area was large enough to allow fishes to escape capture with the quadrat sampler). Fish were collected within the blocked-off area following the 1-m² quadrat sampler using the previously described standardized procedure. To minimize any influence of the block nets on quadrat sampler efficiency, quadrat subsamples were not collected within 1 m of either block net so that fishes could evade capture in any direction. The blocked-off area then remained undisturbed for more than 30 min (average = 62 min) to allow those fishes remaining in the blocked-off riffle to settle down; Bain et al. (1985) found that 15 min was adequate for fishes to recover following installation of prepositioned area electrofishers. Fishes were then sampled in the blocked-off riffle with a secondary gear, an electric seine (Bayley et al. 1989). The electric-seine sample consisted of fishes collected during two passes—the first upstream, the second downstream—and any fish that may have drifted into the downstream block net during electrofishing.

Physicochemical measurements.—Physical and chemical stream characteristics that may affect quadrat sampler efficiency were measured in each riffle immediately following fish sampling. Water conductance, temperature, and turbidity were measured in the middle of each blocked-off riffle. Mean current velocity and depth were estimated by averaging readings at five randomly selected points within each riffle. Based on a previous assessment (Peterson 1996), we found that five readings were sufficient to fall within 10% of the “true” mean depth and current velocity with 95% confidence. Velocity was measured at a depth of 0.6 m with a Marsh McBirney model 2000 water-current meter attached to a standard, top-set wading rod. The percentage of riffle covered with vegetation, woody debris (e.g., logs), cobble (20–200 mm diameter), and boulder (>200 mm diameter) substrate was visually estimated. The percentage of area sampled by the quadrat sampler was estimated by dividing the total area sampled by the area of the blocked-off riffle.

Definitions and statistical analysis.—Within each blocked-off riffle, quadrat sampler fish abundance (QA) was estimated by multiplying quadrat-

specific density estimates for each species by the area of the blocked-off riffle. Species richness was estimated as the sum of the total number of species collected with the quadrat sampler (i.e., all subsamples). Reliable estimates of fish abundance and species richness in the blocked-off riffle were then obtained by adjusting the electric-seine catch with gear-efficiency models from Bayley and Dowling (1990) as adjusted by Peterson (1996), that is,

$$T = N/\pi + Q,$$

where T = estimated number of fish per species or total number of species, π = predicted electric-seine efficiency as a fraction, N = the number of fish or species collected with the electric seine, and Q = the total number of fish removed from the site (collected) during sampling with the quadrat sampler. Predicted electric-seine sampling efficiency (π) was estimated by the use of sampling-efficiency models from Bayley and Dowling (1990) that were adjusted for Ozark species and verified (Figure 2) by Peterson (1996).

The QA and T , rounded down to the nearest whole number, were used as dichotomous, dependent variables (i.e., the number of success and trials, respectively) for the logistic regression-modeling procedure described below. Note that on several occasions, one or more individuals in a family (size) group were collected with the electric seine but not with the quadrat sampler. In these instances, the number of successes equaled zero and the number of trials equaled the number of individuals captured with the electric seine. Thus, data for all sizes and species captured (except Fundulidae and Centrarchidae, see Results) were used for the modeling procedure. Pearson correlations were run on all pairs of predictor variables (i.e., physicochemical measurements). To avoid multicollinearity, predictor variables that were significantly correlated ($P < 0.1$) were not used together in the modeling procedure.

Efficiency differences among species were examined by separating species into family groups. Differences among families were then examined by treating each family as a covariate in the quasi-likelihood regression models, outlined below. Significantly different families ($P < 0.05$) were analyzed separately, and individual differences among species within a family were similarly examined.

Because fish length affects the efficiency of many collection methods (Bagenal 1979; Reynolds 1996), species groups were separated into 30-mm

length-groups. The inverse of the average length of fishes in a length group (i.e., one group/fish length) was used as a predictor variable in the modeling procedure. For example, assuming that the electric-seine-estimated abundance for a family group was three fish with lengths of 100, 95, and 90 mm, the average length of the 90-mm to 120-mm length group would be 95 mm.

We used logistic regression (Agresti 1990) to estimate the effects of individual predictor variables and combinations of uncorrelated predictor variables on the efficiency of the quadrat sampler. A preliminary examination of the dispersion parameters for best-fitting logistic-regression models indicated the data were overdispersed (i.e., the variance exceeded the presumed binomial). Overdispersion is often associated with modeling fish sampling efficiency due to the nonindependence of fish responses and/or unmeasured factors affecting efficiency (Bayley 1993). To account for the overdispersion, we modeled sampling efficiency with quasi-likelihood regression, which is similar to logistic regression but an additional element: the extra-binomial variance (Williams 1982). Predictor variables were considered statistically significant at $\alpha = 0.05$, and residuals were inspected for outliers and independence.

Following Bayley (1993), predicted quadrat sampler efficiency was calculated as

$$\pi = \{1 + \exp[-(\beta_0 + \beta_1 x_1 + \dots)]\}^{-1},$$

where π = predicted efficiency as a fraction, β_0 is the constant, β_i are the model coefficients, and x_i are the corresponding variable values. Ninety-five percent confidence limits were calculated using the predicted efficiency from equation (2) and the extra-binomial variance

$$\pi^{\text{upper}} = [1 + \exp(-\langle \log_e[\pi/(1 - \pi)] + 1.96\sqrt{p\{[T\pi(1 - \pi)]^{-1} + \sigma^2\}}\rangle)]^{-1},$$

where π is the estimated efficiency, T is the estimated number of fish, and σ^2 is the extra-binomial variance. The lower confidence limit was obtained by changing the plus sign preceding 1.96 to a minus sign.

Results

The 25 quadrat sampler calibrations covered a wide range of habitat characteristics (Table 1) and collected 19 common species in six families (Table 2) found in Ozark streams. However, two of the

TABLE 1.—The means (SE) and range of physical habitat variables for the 25 1-m² quadrat sampler calibrations in the Jack Forks River, Missouri.

Habitat characteristic	Mean	Range
Length (m)	12.6 (0.52)	11–15
Mean width (m)	6.2 (0.41)	3–15
Mean depth (cm)	15.4 (1.22)	5–28
Mean velocity (m/s)	0.6 (0.10)	0.16–1.10
Conductivity (μ S)	289.0 (8.64)	150–390
Temperature ($^{\circ}$ C)	18.2 (1.35)	9.5–29
Percent vegetation	1.3 (0.76)	0–15
Percent boulder	4.6 (1.46)	0–25
Percent cobble	45.6 (5.14)	10–75
Percent area sampled	17.9 (0.19)	8.3–22.7

families, Fundulidae and Centrarchidae, were each represented by a single species collected with the electric seine on one or two occasions in numbers ranging from 1 to 2 individuals. Fishes in four family groups were collected in sufficient numbers by both the quadrat sampler and electric seine to accomplish reliable calibrations. All of the species were used to estimate species-richness efficiency.

Pearson correlations for all possible pairs of the 10 habitat-predictor variables (Table 1) indicated significant correlations between mean depth and velocity ($P = 0.03$) and temperature and conductivity ($P = 0.009$). In addition, percent area sampled, site width, and length were significantly intercorrelated ($P = 0.08$).

Average fish length, fish family membership, and the ten habitat-predictor variables were evaluated individually and in various combinations with quasi-likelihood logistic regression. Mean velocity ($P < 0.001$), temperature ($P = 0.003$), and percent cobble ($P = 0.01$) were significantly and negatively correlated with quadrat sampler efficiencies. In addition, there were significant differences among families ($P < 0.001$) as well as significant family \times temperature ($P < 0.01$) and family \times percent cobble ($P < 0.05$) interactions. There was no statistically significant length effect ($P > 0.05$), and consequently the groups were pooled over fish length (i.e., one data point per species per calibration).

Quadrat sampler efficiency was then evaluated separately for each fish family (Table 2) with quasi-likelihood logistic regression that used various combinations of the 10 pairs of habitat-predictor variables and species family membership. Mean current velocity significantly and negatively influenced sampling efficiencies for Cyprinidae ($P = 0.009$), Cottidae ($P = 0.006$), and Percidae ($P < 0.001$; Table 3), but not Ictaluridae ($P = 0.47$). Percent cobble also negatively influenced sam-

TABLE 2.—Number of calibrations (*N*) and the mean and range of total length for all species collected in the Jack Forks River, Missouri, by method, during the calibration procedure.

Family and species		Total length (mm)					
		Quadrat sampler			Electric seine		
		N	Mean	Range	N	Mean	Range
Cyprinidae							
Ozark chub	<i>Erimystax harrisi</i>	5	63	43–88	5	79	45–106
Rosyface shiner	<i>Notropis rubellus</i>	0			2	59	53–65
Telescope shiner ^a	<i>N. telescopus</i>	0			1	59	
Bleeding shiner	<i>Luxilus zonatus</i>	25	46	27–88	25	57	26–111
Ozark shiner	<i>N. ozarcanus</i>	5	42	36–51	5	54	45–73
Ozark minnow ^a	<i>N. nubilus</i>	0			1	51	
Largescale stoneroller	<i>Camptostoma oligolepis</i>	21	57	32–113	21	58	29–121
Ictaluridae							
Yellow bullhead ^a	<i>Ameiurus natalis</i>	0			1	30	
Slender madtom	<i>Noturus exilis</i>	19	53	24–76	19	51	27–95
Ozark madtom	<i>N. albatris</i>	24	61	21–98	24	53	28–95
Fundulidae							
Northern studfish ^a	<i>Fundulus catenatus</i>	0			2	78	37–112
Cottidae							
Ozark sculpin	<i>Cottus hypselurus</i>	4	46	32–67	4	40	30–52
Banded sculpin	<i>C. caroliniae</i>	21	62	26–129	21	54	27–142
Centrarchidae							
Smallmouth bass ^a	<i>Micropterus dolomieu</i>	0			1	76	
Percidae							
Arkansas saddled darter	<i>Etheostoma euzonum</i>	9	60	33–83	9	65	36–91
Banded darter	<i>E. zonale</i>	2	54	51–57	2	56	51–62
Rainbow darter	<i>E. caeruleum</i>	25	45	23–68	25	47	26–74
Current darter	<i>E. uniporum</i>	0			2	47	42–51
Fantail darter	<i>E. flabellare</i>	4	41	19–59	6	42	26–62

^a Species collected in less than three calibrations and not included in analyses.

pling efficiencies for Cyprinidae ($P = 0.025$), Ictaluridae ($P < 0.001$), and Percidae ($P < 0.001$), while water temperature negatively influenced sampling efficiency for Cyprinidae ($P < 0.001$) and Ictaluridae ($P = 0.006$; Table 3). There were no statistically significant differences ($P > 0.05$) among species within each family.

Predictor variables were also evaluated individ-

ually and in various combinations with quasi-likelihood logistic regression using estimated species richness (i.e., from electric-seine efficiency-adjusted data) and the number of species collected with the quadrat sampler as the dichotomous dependent variables. Percent area sampled was significantly and positively ($P = 0.002$) related to species-richness efficiency (Table 3).

TABLE 3.—Coefficients for 1-m² quadrat sampler efficiency models with standard error (SE), change in deviance, χ^2 probability, and extrabinomial variance (σ^2) for species groups at the Jacks Fork River, Missouri.

Family and category	Number of calibrations	Variable	Coefficient (SE)	Change in deviance	Two-tailed $P(\chi^2)$	σ^2
Cyprinidae	25	Constant	3.734 (0.977)			0.848
		Mean velocity (m/s)	−0.091 (0.042)	6.92	0.009	
		Temperature (°C)	−0.096 (0.031)	16.04	<0.001	
		Percent cobble	−0.004 (0.002)	5.03	0.025	
Ictaluridae	25	Constant	8.960 (5.925)			0.277
		Temperature (°C)	−0.433 (0.196)	7.46	0.006	
		Percent cobble	−0.041 (0.015)	12.52	<0.001	
Cottidae	21	Constant	1.754 (2.009)			0.397
		Mean velocity (m/s)	−0.700 (0.055)	7.54	0.006	
Percidae	25	Constant	1.301 (0.694)			0.227
		Mean velocity (m/s)	−0.241 (0.037)	49.06	<0.001	
		Percent cobble	−0.019 (0.007)	12.34	0.001	
Species richness	25	Constant	−0.860 (0.592)			0.309
		Percent area sampled	0.068 (0.028)	10.50	0.002	

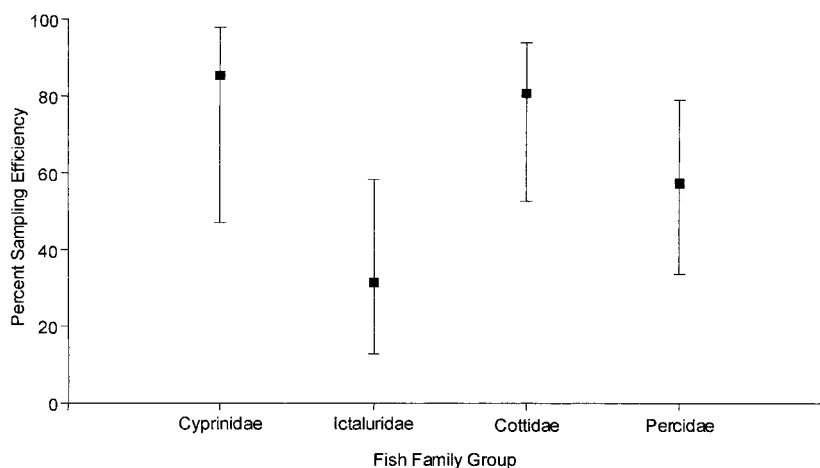


FIGURE 3.—Predicted quadrat sampler efficiencies and 95% confidence intervals for four families of riffle-dwelling fishes in the Jack Forks River, Missouri, under average habitat conditions (see Table 1).

Our efficiency models estimate that, under average habitat conditions encountered in Ozark stream riffles (Table 1), the quadrat sampler was most efficient at estimating the densities of Cyprinidae (84%) and Cottidae (80%) and least efficient for Ictaluridae (31%; Figure 3). However, efficiency estimates for Cyprinidae were also the most variable among the six families (extra-binomial variance = 0.848). Efficiencies for determining species richness were only influenced by the amount of area sampled, which in this study

was expressed as the percent of riffle sampled (Figure 4). We estimate that the quadrat sampler is successful at collecting 60% of the species in a given riffle (i.e., species-richness efficiency) under average sampling conditions (i.e., when 18% of a riffle is sampled, PAS).

Discussion

Accurate estimates of fish species density or richness are only obtained when the biases inherent in sampling are known and accounted for. Biases can only be accurately determined when true population values are known. While numerous studies describe sampling of riffle habitats for fish, only Fisher (1987) examined the efficiency of his gear. Fisher (1987) evaluated an enclosed benthic sampler and whether electrofishing or substrate disturbance (i.e., kick-sampling) within the sampler collected more individuals and species. However, Fisher (1987) only evaluated his primary gear (i.e., the quadrat sampler) and assumed that his secondary method, sodium cyanide plus electrofishing, was 100% effective. This, presumably, is why our average sampling efficiencies for benthic species (i.e., Ictaluridae, Cottidae, and Percidae), 56%, was slightly lower than Fisher's 69%. Additionally, Fisher (1987) did not examine the effects of habitat characteristics on efficiency, nor did he assess the difference in catchability among species. Nevertheless, the overall conclusions from his study and ours show good correspondence.

Sampling Efficiency

There were significant differences in quadrat sampler efficiency among the various families of

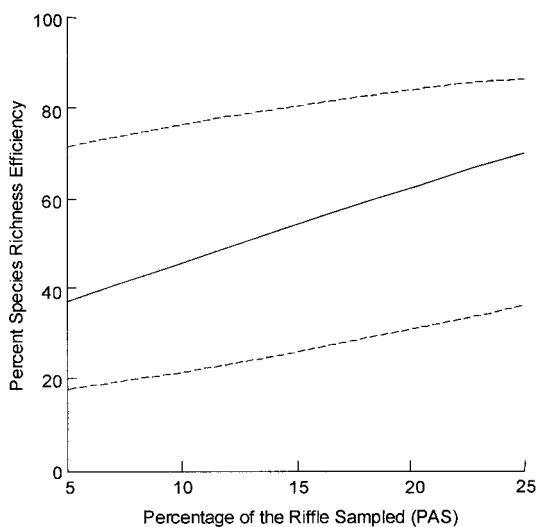


FIGURE 4.—The predicted species richness efficiency (solid line) and 95% confidence intervals (broken lines) for the quadrat sampler under various levels of sampling effort, expressed as the percentage of riffle area sampled in the Jacks Fork River, Missouri.

riffle-dwelling fishes; this was probably due to a combination of morphological and behavioral characteristics. The quadrat sampler was most efficient at capturing Cyprinidae and Cottidae and least efficient at collecting Ictaluridae and Percidae (Figure 3). Ictaluridae and Percidae tended to hide in interstitial spaces in coarse gravel or beneath large, cobble-sized substrate (Pflieger 1997). This made them more difficult to capture than fish in the other family groups. The greater efficiencies in collecting Cottidae may have been due to their morphological adaptations and sedentary nature. Among the species represented, *Cottus caroliniae* and *C. hypselurus*, are cryptically colored and possess large pectoral fins that allow them to withstand strong currents (Pflieger 1975). Cottidae were probably not as disturbed by the sampling procedure as other species. On several occasions, we observed these species remaining motionless on the bottom until physically disturbed.

In contrast, Cyprinidae do not have morphological adaptations to maintain position in high currents (Pflieger 1975), which suggests they should have had greater mobility and an increased ability to avoid capture. We believe high efficiency might have been due to Cyprinidae's use of limited current refugia and a rather clumped distribution, which made them more vulnerable to capture. We observed cyprinids patchily distributed in riffles; most individuals were restricted to a few small areas of reduced current immediately behind boulders or near concentrations of very large cobble. This clumped distribution usually resulted in either many individuals being collected or few or no fish being collected; hence, there was a large extrabinomial variance (Table 3). To minimize the effect of clumped-distribution patterns on density estimates, we recommend that the percent area sampled be as large as possible.

In contrast to previous studies of sampling-gear efficiencies (Buttiker 1992; Bayley and Dowling 1993; Anderson 1995), fish body length did not measurably affect the quadrat sampler's efficiency. We collected a greater number of larger-sized cyprinids with the electric seine (Table 2), but they were not very abundant, which probably affected our ability to detect a length effect. Additionally, we collected very few fish smaller than 25 mm during the calibration procedure (Table 2), which suggests that the quadrat sampler might have been poor at collecting very small fish. Presumably, lower efficiencies for very small fish would have been, in part, due to fish escaping through the 6-mm-mesh collection bag. The block nets used in

the calibration procedure were the same size and would also have allowed very small fish to escape. Consequently, we may have been unable to obtain reliable estimates of very small fish abundance and hence were unable to detect a length effect. A smaller-mesh collection bag may result in greater efficiency for these species, but we caution that altering the design of the quadrat sampler may unintentionally change other sampling characteristics and render our efficiency estimates useless.

Physical habitat characteristics, individually and in combination, significantly affected the quadrat sampler's efficiency. Cobble negatively affected quadrat efficiency for Cyprinidae, Ictaluridae, and Percidae (Table 3). Large amounts of cobble in the riffles impaired the quadrat sampler's ability to seal off the stream bottom, which resulted in gaps that could have allowed fishes to escape. In addition, large amounts of cobble could have provided refuge for fishes and effectively lowered the ability of the person sampling to dislodge the fish and wash them into the collection bag. Current velocity also had a negative effect on sampling efficiency for certain families (Table 3). Higher velocities may have helped fish to escape by speeding their escape out of the 1-m² area before the sampler was in place. It was also difficult to secure the sampler to the streambed in riffles with very high current velocities (>1 m/s), which may have allowed fish to escape. The effect of high current velocities was more pronounced in relatively deep riffles (>0.25 m), where we found that the current continuously applied lift to the front of the sampler. To ensure effective sampling, we suggest that the quadrat sampler not be used in riffles with mean current velocities greater than 1 m/s or with mean depths greater than 0.25 m.

Temperature negatively influenced quadrat sampler efficiency for Cyprinidae and Ictaluridae (Table 3). This may explain why Fisher's (1987) quadrat kick-sampling efficiencies were lower in summer than in other seasons. Previous studies of fish sampling or visual-counting efficiency (Bayley and Dowling 1990; Rodgers et al. 1992; Thurow and Schill 1996) attributed the effects of temperature to its effect on fish activity, which is positively related to water temperature (Windell 1978). Thus, increased water temperature may have led to increased mobility, which increased the ability of fish to avoid capture.

Sampling efficiency for determining the abundance of each of the families of fish was relatively unaffected by the number of subsamples taken. However, the efficiency for determining species

richness (i.e., the total number of species collected compared with the actual number of species in a riffle) was only influenced by the number of subsamples, expressed as the percentage of riffle sampled. We believe that a species–area effect was responsible for this relation. In general, larger areas contain more species (Connor and McCoy 1979). Thus, in proportion to the whole riffle, an increase in the area sampled would have increased the probability of capturing an individual of another species.

We conclude that the 1-m² quadrat sampler is useful for sampling fishes in Ozark stream riffles under a variety of conditions, ranging from small, low-gradient riffles in headwater streams, to relatively large, high-gradient riffles in mainstem reaches. A species' morphology and behavior and the physical habitat characteristics of riffles, both of which may be specific to the Ozark region, influenced the efficiency of the sampler. However, many of our conclusions should be generally applicable to other warmwater stream systems.

One advantage of the quadrat sampler is that a single person can quickly collect samples; a riffle (18% PAS or 12 subsamples) could be sampled in about 15 min. We have previously determined that, on average, 12 riffles need to be sampled to ensure estimates for a stream site with $\pm 20\%$ precision (Peterson and Rabeni 1995). A single individual could obtain estimates of total fish biomass (across species) for each site in approximately 3 h, which is rapid when compared to maximum-effort methods that require several runs. In addition, fish mortality while using the quadrat sampler was always less than 5%. The efficiency of the quadrat sampler was influenced by species type (i.e., family) and physical habitat characteristics. However, by applying efficiency models, we were able to adjust raw catch data to account for these effects. Therefore, we recommend use of the quadrat sampler when a rapid, nonlethal method is needed for estimating the biomass, density, or species richness of riffle-dwelling fishes. We also encourage those conducting stream fish studies to evaluate the efficiency of their fish collection methods and, if necessary, to synthesize gear-efficiency models so that conclusions will be based on unbiased data.

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References

- Agresti, A. 1990. Categorical data analysis. Wiley, New York.
- Anderson, C. 1995. Measuring and correcting for size selection in electrofishing mark-recapture experiments. *Transactions of the American Fisheries Society* 124:663–676.
- Bagenal, T. B. 1979. EIFAC fishing gear intercalibration experiments. United Nations Food and Agriculture Organization, European Inland Fisheries Advisory Council Technical Paper 34, Rome.
- Bain, M. B., and J. T. Finn. 1991. Analysis of microhabitat use by fish: investigator effect and investigator bias. *Rivers* 2:57–65.
- Bain, M. B., J. T. Finn, and H. E. Booke. 1985. A quantitative method for sampling riverine microhabitats by electrofishing. *North American Journal of Fisheries Management* 5:489–493.
- Bart, H. L. Jr. 1989. Fish habitat associations in an Ozark stream. *Environmental Biology of Fishes* 24: 173–186.
- Bayley, P. B. 1993. Quasi-likelihood estimation of marked fish recapture. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2077–2085.
- Bayley, P. B., and D. J. Austen. 1990. Modeling the sampling efficiency of rotenone in impoundments and ponds. *North American Journal of Fisheries Management* 10:202–208.
- Bayley, P. B., and D. C. Dowling. 1990. Gear efficiency calibrations for stream and river sampling. Illinois Natural History Survey, Aquatic Ecology Technical Report 90/08, Champaign.
- Bayley, P. B., and D. C. Dowling. 1993. The effects of habitat in biasing fish abundance and species richness estimates when using various sampling methods in streams. *Polskie Archiwum Hydrobiologii* 40:5–14.
- Bayley, P. B., R. W. Larimore, and D. C. Dowling. 1989. The electric seine as a fish sampling gear in streams. *Transactions of the American Fisheries Society* 118: 447–453.
- Bowen, Z. H., and M. C. Freeman. 1998. Sampling effort and estimates of species richness based on prepositioned area electrofisher samples. *North American Journal of Fisheries Management* 18:144–153.
- Buttiker, B. 1992. Electrofishing results corrected by selectivity functions in stock size estimates of brown trout (*Salmo trutta* L.) in brooks. *Journal of Fish Biology* 41:673–684.
- Connor, E. F., and E. D. McCoy. 1979. The statistics and biology of the species area relationship. *American Naturalist* 113:791–833.
- Coon, T. G. 1987. Responses of benthic riffle fishes to variation in stream discharge and temperature. *Page-*

- es 298–325 in W. S. Matthews and D. C. Heins, editors. *Community and evolutionary ecology of North American stream fishes*. Oklahoma University Press, Norman.
- Ensign, W. E., P. L. Angermeier, and C. A. Dolloff. 1995. Use of line transect methods to estimate abundance of benthic stream fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 52:213–222.
- Fisher, W. L. 1987. Benthic fish sampler for use in riffle habitats. *Transactions of the American Fisheries Society* 116:768–772.
- Greenberg, L. A. 1991. Habitat use and feeding behavior of thirteen species of benthic stream fishes. *Environmental Biology of Fishes* 31:389–401.
- Kessler, R. K., A. F. Casper, and G. K. Weddle. 1995. Temporal variation in microhabitat use and spatial relations in the benthic fish community of a stream. *American Midland Naturalist* 134:361–370.
- Lotrich, V. A. 1975. Growth, production and community composition of fishes inhabiting a first-, second-, and third-order stream of eastern Kentucky. *Ecological Monographs* 43:378–397.
- Lyons, J. 1986. Capture efficiency of a beach seine for seven freshwater fishes in a north-temperate lake. *North American Journal of Fisheries Management* 6:288–289.
- Peterson, J. T. 1996. The evaluation of a hydraulic unit-based habitat classification system. Doctoral dissertation. University of Missouri, Columbia.
- Peterson, J. T., and C. F. Rabeni. 1995. Optimizing sampling effort for sampling warmwater stream fish communities. *North American Journal of Fisheries Management* 15:528–541.
- Pflieger, W. L. 1997. *The fishes of Missouri* (revised). Missouri Department of Conservation, Jefferson City.
- Rabeni, C. F. 1985. Resource partitioning by stream dwelling crayfish: the influence of body size. *American Midland Naturalist* 113:20–29.
- Reynolds, J. B. 1996. Electrofishing. Pages 221–254 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Riley, S., R. Haedrich, and R. Gibson. 1993. Negative bias in removal estimates of Atlantic salmon parr relative to stream size. *Journal of Freshwater Ecology* 8:97–101.
- Rodgers, J. D., M. F. Solazzi, S. L. Johnson, and M. A. Buckman. 1992. Comparison of three techniques to estimate juvenile coho salmon populations in small streams. *North American Journal of Fisheries Management* 12:79–86.
- Schlösser, I. J. 1981. Trophic structure, reproductive success, and growth rate of fishes in a natural and modified headwater stream. *Canadian Journal of Fisheries and Aquatic Sciences* 39:968–978.
- Thurrow, R. F., and D. J. Schill. 1996. Comparison of day snorkeling, night snorkeling, and electrofishing to estimate bull trout abundance and size structure in a second-order Idaho stream. *North American Journal of Fisheries Management* 16:314–323.
- Weddle, G. K., and R. K. Kessler. 1993. A square meter electrofishing sampler for benthic riffle fishes. *Journal of the North American Benthological Society* 12:291–305.
- Williams, D. A. 1982. Extra-binomial variation in logistic-linear models. *Applied Statistics* 31:144–148.
- Windell, J. T. 1978. Digestion and the daily ration of fishes. Pages 159–183 in S. D. Gerking, editor. *The biological basis of freshwater fish production*. Wiley, New York.